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Bimanual information processing and the impact of conflict during mirror drawing

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Abstract

Successful motor behavior depends on optimal information processing and planning. In the present study, the neural response of the motor system to conflict of visuomotor discrepancy (mirror-reversed vision) and complexity (task difficulty and hand laterality) was evaluated during the performance of bimanual actions. EEG coherence, expressing interregional communication, showed that conflict of visuomotor incongruence resulted in activation changes in both hemispheres, whereas conflict of task complexity evoked adjustments primarily in the left hemisphere. Furthermore, interhemispheric coherence was modified due to both forms of conflict. This demonstrates that conflict demands elicit distinct processes across the motor system. The data further illustrate that functional couplings are dynamically modulated during bimanual behaviour, suggesting that interactions between brain regions provide higher-order links for information processing and integration in view of complex motor skills.

Keywords: EEG, coherence, functional connectivity, task complexity, laterality, visuomotor discrepancy

1. Introduction

Coordinated movements of the hands involve a variety of spatio-temporal combinations and degrees of complexity. Despite high flexibility and common ease of bimanual performance, intrinsic constraints exist that hamper movement organization of intricate skills. Research has demonstrated that at least two forms of coupling arise: temporal and spatial [45]. Their existence imposes symmetry of action as preferred between-hand association, resulting in low task complexity. However, performance difficulties arise when asymmetrical acts are required such as when moving the hands with dissimilar tempo or spatial requirements. In this case, assimilation or interference occurs [16,27]; an effect that is sensitive to handedness-related asymmetries, enabling the dominant limb to exert a stronger influence on the non-dominant limb than vice versa [9,13]. During motor behaviour, vision and proprioception are critical sources of information that interact for planning, execution and monitoring of performance. This becomes most evident when exposed to environments during which visual and proprioceptive signals diverge. In this case, motor output is often disrupted. One such example is mirror drawing during which a two-folded conflict situation is created that involves an incongruence of visuoproprioceptive information processing [28] and a discrepancy of visuomotor regulation [32]. It accordingly implies concurrent processes of adaptation that include sensory recalibration and strategic control modifications [37].

In the present study, bimanual coordination is examined under situations of conflict. In particular, an evaluation is made about changes in neural activity due to conflict of visuomotor incongruence (mirror-reversed vision) and complexity (task difficulty and hand laterality). As an approach to describe brain activity, the data analysis focuses on EEG coherence that expresses functional communication between brain areas [1,17,41]. The hypothesis was made that if task-related processes are mediated by modulations in interregional connectivity, then neural activation of bimanual patterns would be dynamically adjusted in view of the conflict demands. Moreover, the argument was made that the distinctive nature of the type of conflict would induce selective information processing across the motor system.

2. Materials and methods

2.1. Subjects

Nine right-handed individuals (age: 20.8±1.4 years) as determined by the Edinburgh handedness inventory [35] with no history of neurological disease participated in the experiment. In accordance with the declaration of Helsinki, the participants gave informed consent to take part in the study, which was approved by the local ethics committee.

2.2. Tasks and procedure

The participants were asked to perform continuous bimanual drawing movements that involved different degrees of complexity. Two basic shapes cut out of paper were used; an oblique line and a triangle, with each single segment involving a path length of 10 cm and a line width of .80 cm. The topological nature of the triangle made its tracing more complex than the line, due to the number of distinct directional changes at corner points. Previously, a linear relationship between tracing time and number of corners has been observed, with time costs at the corner points [32] which also associate with velocity minima [18]. The combination of the line and triangle templates resulted in 4 bimanual tasks with different levels of complexity. Condition 1 = oblique line + oblique line, condition 2 = oblique line + triangle, condition 3 = triangle + oblique line, condition 4 = triangle + triangle. Based on task complexity, the conditions were subsequently labeled as: Condition 1 = easy both, condition 2 = complex right, condition 3 = complex left, condition 4 = complex both). All the bimanual tasks were performed under 2 experimental conditions that combined normal vision for one hand and mirror-inverted vision for the other hand, i.e., resulting in left hand mirror and right hand mirror movements. In addition, control conditions were executed that involved the bimanual patterns with similar kinematics as those performed in the experimental conditions, but without mirror. Subjects first performed the control conditions followed by the experimental conditions (counterbalanced order). In the control and experimental conditions, the order of the bimanual tasks was counterbalanced.

Participants performed the drawing tasks on two small Wacom writing tablets (200 x 185 x 11 mm), using ink- and wireless pens. The pen trajectories were acquired in x- and y-coordinates, and stored for off-line analysis. Behind the drawing tablets, a mirror with semi-silvered coated properties was placed. In the experimental conditions, a template was positioned behind the mirror such that the reflection of the image could be used to produce the mirror-inverted drawing on one tablet, whereas the template of the normal image was positioned on the other tablet. Accordingly, the drawing tasks enabled tracing onto the templates. The start positions of both images were fixed and spatially aligned, and the initial direction of both movements was also indicated. Instructions were provided to trace both templates simultaneously and continuously for the duration of the trial, as fast and as accurately as possible. Trials lasted 40 s each, and there were 2 trials per bimanual task. Practice with and without the mirror set-up was provided. There were small breaks in between trials for avoiding fatigue and loss of attention. Participants were told in advance of the upcoming task requirements. A rest condition was also recorded.

2.3. EEG recordings and data analysis

Continuous EEG was recorded using the Electrical Geodesics Inc. 128-channel system, and data processing was carried out using BESA software (MEGIS Software GmbH, Gräfelfing, Germany). EEG signals were amplified, band-pass filtered 0.05 Hz–100 Hz, and sampled at 250 Hz with a vertex reference. Epochs contaminated by artifacts such as eye movements and EMG-related activity were corrected for or rejected after baseline correction.

EEG coherence was used to assess functional connectivity between brain areas in the frequency domain, and was estimated by means of complex demodulation set to a frequency resolution of 2 Hz and temporal resolution of 25 ms. Background coherence acquired during rest was subtracted from coherence obtained during motor conditions. This method, which gives an estimate of task-related coherence, reduces the effects of volume conduction, between-subject differences as well as between-electrode variability, and minimizes the bias introduced by the reference electrode. As a normalized measurement of coupling between two signals at any given frequency, coherence varies between 0 (no correlation) and 1 (perfect correlation).

To measure indices of cortical activity, a region of interest approach was adopted that focused on a restricted number of electrodes. The electrodes were selected based on earlier EEG studies of movement control [10,24,40] and were estimated to overlie premotor, sensorimotor and parietal areas. The division of electrodes resulted in the following connectivity groupings characterizing the motor system: intrahemispheric left (FC3-C3, FC3-CP3, FC3-P3, C3-CP3, C3-P3, CP3-P3), intrahemispheric right (FC4-C4, FC4-CP4, FC4-P4, C4-CP4, C4-P4, CP4-P4), interhemispheric (FC3-FC4, C3-C4, CP3-CP4, P3-P4). Coherence was evaluated in the beta frequency band (>12-30 Hz) due to its importance for motor behavior [17,43]. Before statistical operations were conducted, coherences were transformed using the inverse hyperbolic tangent to stabilize variances. In addition, EEG task-related power (obtained by subtracting rest from the corresponding motor conditions) was measured in the beta band at the individual electrodes, and stabilized by logarithmic transformation. Subsequently, power was analyzed in conjunction with coherence measurements in order to evaluate whether changes in power could have contributed to the modulations in coherence. Non-significant effects would indicate that power changes were not primarily responsible for coherence modulations, suggesting that the motor system effectively responded by changing interregional communication. Mean ± SD scores are presented in the Results section.

2.4. Behavioural recordings and data analysis

E-Prime software (Psychology Software Tools Inc., Pittsburgh, USA) was used to record the trajectories. The total path length for the trial durations was determined for each task condition and used as an estimate of behavioural performance.

2.5. Statistical analysis

The data were analyzed using Statistica software (StatSoft Inc., Tulsa, USA). Adjustments were made in case of violation of the sphericity assumption by using the Greenhouse-Geisser procedure. Post-hoc testing included corrections with respect to multiple comparisons.

3. Results

3.1. EEG coherence

The EEG analysis was conducted separately for the intrahemispheric and interhemispheric couplings.

3.1.1. Intrahemispheric coherence

To evaluate the impact of the mirror manipulation, percentage scores were calculated with the degree of intrahemispheric coherence during the control conditions set at 100%. Overall, intrahemispheric coherence increased significantly during both mirror conditions, as confirmed by one sample *t*-tests ($p<0.05$). The mean left-right hemisphere scores were 127±14% and 115±10% for the left hand mirror condition, 118±12% and 111±8% for the right hand mirror condition.

The evaluation of the bimanual tasks in both mirror conditions was made through a 4 x 2 x 2 ANOVA on task (easy both, complex right, complex left, complex both), mirror (left hand, right hand) and hemisphere (left side, right side). The analysis revealed a significant main effect of task [$F(3,24)=25.93$, $p<0.01$], and hemisphere [$F(1,8)=77.45$, $p<0.01$]. The task x hemisphere interaction was significant [$F(3,24)=8.72$, $p<0.01$]. Post-hoc analysis indicated that for the dominant (left) hemisphere, activation intensified as a function of augmented task complexity, whereas for the non-dominant (right) hemisphere ($p<0.05$), the easy both tasks differed from the more complex tasks ($p<0.05$), which did not differ from one another ($p>0.05$). Hence, there was a targeted coherence increase due to task complexity in the dominant as compared to non-dominant hemisphere (Fig. 1, left panel). The mirror x hemisphere interaction was significant [$F(1,8)=12.71$, $p<0.01$]. Post-hoc analysis revealed that the left hand mirror compared to right hand mirror movements induced increased coherence in the left hemisphere ($p<0.05$), but not in the right hemisphere ($p>0.05$). This observation illustrates that complexity due to hand laterality primarily impacted on the activation of the dominant hemisphere (Fig. 1, right panel).

Insert Fig. 1 about here

3.1.2. Interhemispheric coherence

To assess the effect of the mirror manipulation, percentage scores were computed with the degree of interhemispheric coherence during the control conditions set at 100%. Overall, interhemispheric coherence increased significantly during both mirror conditions, as confirmed by one sample *t*-tests ($p<0.05$). The mean scores across tasks were 130±16% and 114±13% for the left hand mirror and right hand mirror condition.

The assessment of the bimanual tasks in both mirror conditions was conducted through a 4 x 2 ANOVA on task (easy both, complex right, complex left, complex both) and mirror (left hand, right hand). The analysis showed a significant main effect of task [$F(3,24)=5.64$, $p<0.01$]. Post-hoc analysis revealed that the easy both tasks generated less coherence than the more complex tasks ($p<0.05$), which did not differ from one another ($p>0.05$), (Fig. 2, left panel). There was also a main effect of mirror [$F(1,8)=191.44$, $p<0.01$], with left hand mirror movements inducing a higher degree of coherence than right hand mirror movements (Fig. 2, right panel). Together, these data indicate that complexity due to task and hand laterality resulted in increased functional connectivity between both hemispheres.

Insert Fig. 2 about here

3.2. EEG power

Correlation analyses between the coherence scores of the intrahemispheric and interhemispheric couplings and the power scores of the individual electrodes demonstrated no significant effects, $p>0.05$. The mean correlation coefficients for left hand mirror movements were 0.20, -0.03, -0.22, -0.04 for easy both, complex right, complex left, and complex both. The mean correlation coefficients for right hand mirror movements were 0.11, -0.05, -0.23, 0.07 for easy both, complex right, complex left, and complex both.

3.3. Behavioural path length

To estimate the effect of the mirror manipulation, percentage scores were calculated with the amplitude during the control conditions set at 100%. Overall, amplitude decreased significantly during both mirror conditions, as confirmed by one sample *t*-tests ($p<0.05$). The mean scores across tasks were 73±7% and 84±9% for left hand mirror and right hand mirror conditions.

The evaluation of the bimanual tasks in both mirror conditions was made with a 4 x 2 x 2 ANOVA on task (easy both, complex right, complex left, complex both), mirror (left hand, right hand) and effector (left hand, right hand). The analysis demonstrated a significant main effect of task [$F(3,24)=50.99$, $p<0.01$], mirror [$F(1,8)=12.84$, $p<0.01$], and effector [$F(1,8)=4.98$, $p<0.05$]. There was a task x mirror interaction [$F(2,16)=5.64$, $p<0.01$]. Post-hoc analyses showed that amplitude in the easy both tasks was similar during both mirror conditions ($p>0.05$), whereas amplitude was reduced during left hand mirror compared to right hand mirror movements in the more complex tasks ($p<0.05$). The mean scores for the left hand mirror and right hand mirror conditions were 134±16cm and 129±14cm, 95±13cm and 106±10cm, 84±9cm and 98±13cm, 82±15cm and 100±11cm for easy both, complex right, complex left, and complex both. The task x effector interaction was also significant, [$F(1,8)=5.08$, $p<0.05$. Post-hoc analyses demonstrated that the right hand covered more amplitude than the left hand in the easy both tasks ($p<0.05$), but not in the more complex tasks ($p>0.05$). The mean left-right hand scores were 126±13cm and 135±16cm, 102±9cm and 105±11cm, 92±12cm and 88±10cm, 89±11cm and 91±14cm for easy both, complex right, complex left, and complex both.

4. Discussion

When performing visually guided movements, vision and proprioception inform about the position of the limb. In normal sensory conditions, these estimates correspond, which enables advantageous mapping and planning. In case of incongruent sensory information, the favorable organization is disturbed and motor execution often degrades. This occurs for example when using a mirror during which the visual cues are mirror-reversed with respect to the limb motion. Difficulties arise due to conflict in visuoproprioceptive information processing [4,6,28] and/or visuomotor planning demands [32].

While congruent information processing is crucial in view of movements with one effector, it becomes increasingly important for coordinated behaviour. Accordingly, the present study assessed the impact of conflict due to visuomotor incongruence during bimanual behaviour. To this end, mirror-induced processing during drawing performances was evaluated. In addition, the effect of conflict as a result of complexity (task and hand) was also assessed. The argument was made that the neural dynamics would explicitly change in response to the conflict demands.

4.1. Bimanual drawing and behavioural consequences

Drawing involves multiple complex processes and commonly engages a widespread bilateral activation pattern [22,30]. Support for this finding comes from patient work that has shown that visuospatial tasks are impaired following left as well as right hemisphere lesions [19,49]. This suggests that motor skills with strong sensorimotor demands implicate bi-hemispheric participation [44]. In drawing geometric shapes, as used in the present study, control processes manage the topological characteristics of the shape as well as the spatial characteristics of the components (number of segments and changes in direction), which together exemplify the complexity of the task. The latter is of additional importance when performing bimanual acts during which spatial coupling represents an intrinsic constraint [16,31]. This organization evokes bimanual interactions through a coupling mechanism of which the dominant limb exerts a stronger influence on the non-dominant limb than vice versa [9,13]. The latter asymmetrical arrangement is supported by an inherent attentional bias towards the dominant hand [36], such that strategies that modify this preference also change the trajectories of the individual motions [15,48]. Accordingly, the effects of hand laterality and task constraints yield a significant influence upon the control processes.

The behavioural data indicated that visuomotor discordance resulted in a reduced motor output as compared to control conditions. This suggests slowing down of drawing performance, possibly due to greater monitoring of the trajectories in the conflict conditions. Furthermore, the left hand mirror manipulation perturbed drawing behaviour more strongly than the right hand mirror manipulation as a function of task complexity. In this respect, previous work has shown that visuomotor trajectory regulation is inferior for the left than right hand due to processing and attentional differences [29]. Hence, it is likely that in the left hand mirror conditions, subjects experienced more difficulties to cope with visuomotor incongruence in terms of processing effort and attentional demands due to a preferred perception-action coupling through the dominant hand [8]. Furthermore, the results showed that the superior output of the dominant hand that was evident during the easy tasks disappeared during the more complex tasks. This finding hints at regular realignment of the hand positions due to task complexity, herewith weakening between-hand performance differences. The latter is in line with previous data that have demonstrated that the degree of manual asymmetry diminishes with task complexity [23]. It further is indicative of interactions at high level for controlling hand trajectories in intricate circumstances.

4.2. EEG: Intrahemispheric functional connectivity profiles and response to conflict

The EEG data showed that intrahemispheric coupling changed in response to the conflict situation induced by visuomotor incongruence (mirror) and complexity (task and hand laterality). *First*, visuomotor discordance had a global effect on neural activation patterns. In particular, as compared to control conditions during which both hands received normal vision, the mirror manipulation during which one hand was subject to normal vision while the other hand obtained mirror-reversed vision resulted in augmented intrahemispheric coherence in both hemispheres. This finding appears consistent with sensorimotor adaptation during arm movements, which implicates distributed regions [e.g., 2,11,25]. In the present bimanual context, it is hypothesized that the mirror conditions engaged higher-order control mechanisms in both hemispheres. This is argued to be due to an increased load on the left hemisphere because of its implication in sensorimotor planning, including binding of the spatial and temporal information [3], and on the right hemisphere in view of its involvement in visuospatial processing [47]. Hence, neural response to sensorimotor conflict takes place across both hemispheres, and is expected to be driven by attentional mechanisms of motor attention [39] and spatial attention [12].

Second, complexity expressed by task difficulty and mirror-perturbed hand impacted more strongly on the dominant (left) as compared to the non-dominant (right) hemisphere.

This finding is in agreement with previous data that have indicated left hemisphere dominance for complex actions with either hand [20]. Thus, complexity of motor behaviour is largely addressed by mechanisms that engage the left hemisphere. It reflects superiority of the left hemisphere for regulating the less skilled non-dominant hand and for processing intricate task demands. This observation supports patient work that has shown that damage to the left hemisphere causes bilateral motor deficits as compared to damage to the right hemisphere which results in more restricted contralateral difficulties [21,49].

Together, the findings on conflict demonstrate that visuomotor discrepancy results in pronounced activation changes in both hemispheres, whereas complexity produces marked activation modulations in the dominant hemisphere. This illustrates that the response to conflict occurs through flexible mechanisms that target the motor network in a definite manner.

4.3. EEG: Interhemispheric functional connectivity profiles and response to conflict

The EEG data revealed that conflict from visuomotor incongruence and complexity impacted on the functional transfer between the hemispheres, which supports the premise that interhemispheric interactions provide an important communication pathway for movement regulation and attentional resources [14,46]. In particular, interhemispheric coherence was higher during mirror than control conditions. Furthermore, the effect was most pronounced when the left hand compared to the right hand received the mirror-reversed feedback. This finding indicates an effect of hand laterality and highlights the presence of a bi-directional mechanism that integrates inhibitory influences between both hemispheres. In particular, as the dominant hemisphere is more efficient in inhibiting the non-dominant hemisphere than vice versa [34,43], it accordingly renders the dominant hand less susceptible to influences from the non-dominant hand than vice versa. In addition, task complexity affected the functional coupling between the hemispheres, supporting previous work that has shown that increased task difficulty results in higher interhemispheric coherence [42]. This signifies that communication between the hemispheres tends to intensify as a function of task difficulty. It underlines that interhemispheric information processing becomes increasingly important in challenging conditions for coordinating the resources [5].

Together, the data from the intra- and interhemispheric coupling patterns have provided evidence for distinctive neural responses to conflict situations of sensorimotor incongruence and complexity. The strengthening of the functional couplings across the motor network hints at increased information processing to manage the intricate requirements, and this in association with attentional tactics [26,38]. It is noteworthy that the tasks involved tracing onto the templates, which is expected to have assisted the functional regulation of the drawing activity. However, it is assumed that the modulated activity across the motor network is driven by separate areas such as the anterior cingulate and dorsolateral prefrontal cortex, which guide the responsive dynamics to accommodate the task constraints in conflict conditions [7,33].

Conclusion. Common daily life activities require bimanual coordination patterns, which involve advanced control processes for successful performance. Hence, in case of conflict situations, the normal regulation mechanisms are perturbed, which often leads to degraded behaviour. In the present study, it was shown that the motor system adjusts to conflict demands of visuomotor incongruence and complexity by modifying its functional connectivity profiles within and between hemispheres in a context-dependent way. The data further illustrate that functional couplings are dynamically modulated during bimanual behaviour, suggesting that interactions between distant brain regions provide higher-order links for information processing and integration in view of complex motor skills.

In tracing, the
model and drawing trajectory overlap on the same space, and subjects
can therefore use strategies in the local space
under tracing

difference between copying and tracing/reaching is that the
drawing space is separated from the model space in copying, thus
requiring additional transformation from model to drawing space.

which enables feedback control comparing the model
and drawing trajectory in the same space, whereas subjects have to
produce drawing trajectory on blank space under other conditions,
which therefore requires generation of a mental representation of
the trajectory.

in mental image generation or
motor planning of drawing trajectory.

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Figure Caption

Fig. 1. Left panel: Intrahemispheric coherence of the dominant (left) and non-dominant (right) hemisphere in the different bimanual tasks (EB=easy both, CR=complex right, CL=complex left, CB=complex both). In the left hemisphere, coherence increased steadily as a function of augmented task complexity, whereas the effect was less marked in the right hemisphere. Right panel: Intrahemispheric coherence of the dominant (left) and non-dominant (right) hemisphere in the left hand mirror (LM) and right hand (RM) mirror conditions. Left hand mirror movements compared to right hand mirror movements generated increased coherence in the left hemisphere, but not in the right hemisphere.

Fig. 2. Left panel: Interhemispheric coherence as a function of task complexity (EB=easy both, CR=complex right, CL=complex left, CB=complex both). The easy both tasks produced less coherence than the more complex tasks, which did not differ from one another. Right panel: Interhemispheric coherence as a function of mirror condition (LM=left hand mirror and RM=right hand mirror). Left hand mirror movements generated more coherence than right hand mirror movements.

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Fig. 1

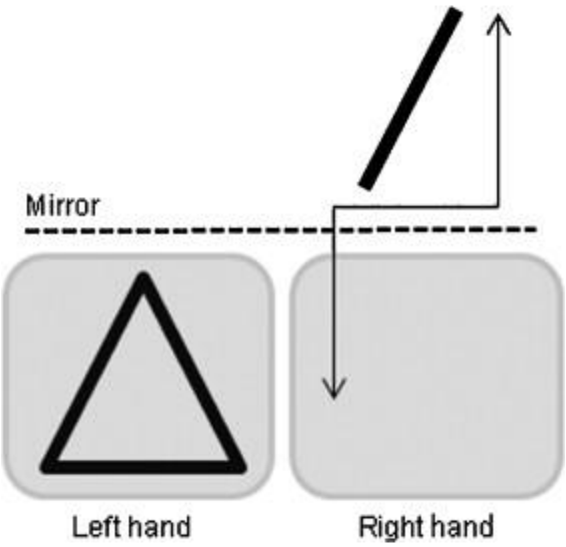
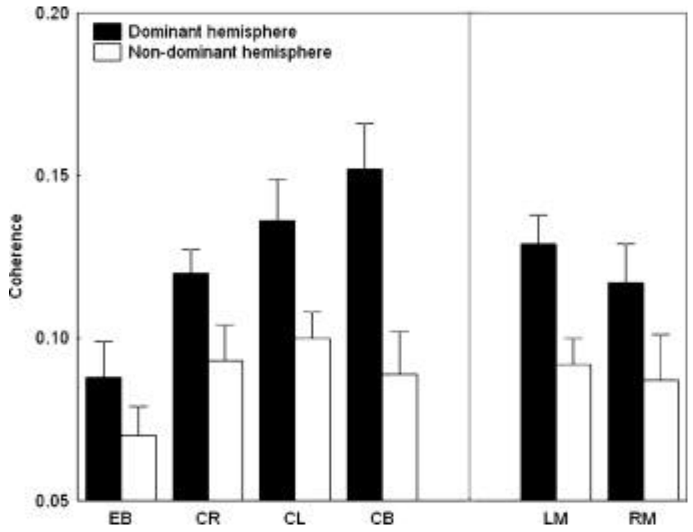


Fig. 2



Dominant hemisphere
Non-dominant hemisphere
0.20
0.15
0.10
0.05
Coherence
EB
CR
CL
CB
LM
RM

Fig. 3